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RESEARCH ARTICLE

Improvising cotton (*Gossypium hirsutum* L.) genotypes for compact plant architecture traits suitable for mechanical harvesting

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Abstract

The study aimed to improve cotton genotypes by developing early maturity and compact plant architecture traits for suitability to high density planting and mechanical harvesting. Ten F_1 populations from five cotton genotypes of Indian origin were developed using a half-diallel mating and evaluated in two seasons (*kharif*, 2022, and Summer, 2023). Results indicated significant genetic variation for all the studied traits, enabling selection and improvement. Combining ability effects interacted significantly with environments. The mean performance of genotypes differed significantly ($p \leq 0.05$), with hybrids outperforming parental genotypes, exhibiting shorter stature and early maturity. The parents, TVH002, and C017 were the best combiners indicated in the hybrids, TVH002 × CO17, and TVH002 × Suraksha for compact plant architecture traits. Non-additive gene action prevailed, as specific combining ability (sca) variances surpassed general combining ability (gca) variances for most studied traits. Genetic components, ratios and heritability revealed that both additive and dominant genes governed the traits, with dominance having a greater influence. Compact architecture traits negatively correlated with seed cotton yield within the 75 to <120 cm height range, resulting in a more stable yield. These findings offer valuable insights for targeted breeding programs aiming to develop compact cultivars with enhanced traits for mechanization and high density cotton plating.

Keywords: Combining ability, cotton, correlation, graphical approach, half diallel, mechanical harvesting

Introduction

In India, mechanical harvesting of cotton is crucial due to labor shortages and high costs of production (Konduru et al. 2013). Plant architecture plays a crucial role in cultural management, affecting the ease and efficiency of practices like manual or mechanical harvesting (Yan et al. 2019). Understanding and manipulating the plant architecture enables researchers to optimize crop geometry leading to higher seed cotton yields and enhanced agricultural sustainability with mechanization. For cotton suitability, shorter plant types are preferred for mechanical harvesting due to challenges posed by excessive vegetative growth and delayed maturity (Venugopalan et al. 2011). Besides plant height, uniformity, shorter sympodial branch length without monopodia, synchronized flowering and uniform boll bursting are important traits. This compact plant canopy is ideal for high density row planting and mechanical harvesting (Gunasekaran et al. 2020). Williford et al. (1994) highlighted the ideal plant heights should be less than 120 cm for spindle pickers and less than 80 cm for stripper pickers.

Data from cotton regions in China, and the US emphasize the importance of a height of first sympodial branch origin over 20 cm to minimize residual defoliant intake and provides optimal space for pickers operation smoothly (Van der Sluijs 2015). Attributes like internode length and sympodial branch

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length have positive and/or negative impacts on yield and harvest efficiency, promoting compact plants (Farias et al. 2016). However, detailed architectural attributes like internode and fruiting branch lengths within the 75 to <120 cm height range have limited information on yield effects. Achieving these goals of key plant architecture traits within the desired height range for mechanical harvesting requires combining desirable genetic traits from diverse genotypes through crossing. In our study, we utilized cotton varieties of Indian origin to develop compact plant types and it is crucial to understand the inheritance of important biometric traits using a half-diallel mating design (Raza et al. 2013; Huangjun and Meyers 2011).

The half-diallel crossing scheme is widely employed in both allogamous and autogamous crops, including cotton (Vasconcelos et al. 2018). This approach enables the evaluation of the general combining ability (*gca*) of parents and the specific combining ability (*sca*) effects of crosses (Berger et al. 2012). Several approaches, such as Griffing's (1956) numerical method and Hayman's (1954) graphical approach, can be used to analyze the data. Through the application of a half-diallel analysis, we gained insights into the genetic characteristics of the parent plants and estimated the gene action for different traits. This approach allowed identifying favorable cross combinations that could lead to compact, earlier crop maturity and high-yielding hybrids is essential for cotton mechanical harvesting. In addition, the correlation among plant architecture traits and seed cotton yield traits suitable for mechanical harvesting were also estimated. The findings are expected to offer valuable insights for crop management and breeding to optimize the plant architecture for high density cotton planting and mechanized harvesting in India.

Materials and methods

Planting materials and experimental location

Five diverse cotton genotypes, namely, TVH002, CO17, NDLH1938, Suraksha, and Nano were chosen as parents for the study considering their distinct quantitative traits. The material source and their selection characteristics are given in Table 1. The hybridization process involved the use of the diallel method, excluding reciprocals (half diallel), resulting in the production of 10 F_1 hybrids during the summer 2022. Hybridization and selfing were executed using manual methods following Doak's (1934) emasculation and hand pollination technique, along with Iyer's (1936) clay smear selfing approach. Stringent measures were implemented to uphold the genetic integrity of each cross both before and after the crosses were made.

The parents and hybrids were evaluated in two different seasons,E_1-*kharif*-2022 and E_2-summer-2023 at the Department of Cotton, Centre for Plant Breeding and Genetics, Tamil Nadu Agricultural University, Coimbatore (latitude: 11.0122°N, longitude: 76.9354°E, elevation: 432.0 and 430.9 m above sea level, respectively). A randomized complete block design (RCBD) with three replications was used for allocating each genotype in two rows of six-meter length with a spacing of 90 × 30 cm (R × P). The recommended package of practices from the TNAU Crop Production Guide was followed for raising the plants.

Observations recorded

Five plants of each genotype were selected randomly from the middle rows of each replication to collect data. The traits, namely, days to 50% flowering, plant density at the harvest the number of plants counted/square meter, plant height measured from the cotyledonary node to the shoot apex using tape (cm), number of monopodia and sympodia branches on the main stem, height of the first sympodia branch origin (cm), sympodial branch length (SBL, cm) (The SBL was divided into three, Fig. 1A): The lower sympodial branches (LSB, 1st–5th branch), middle sympodial branches (MSB, 6th–10th branch), and upper sympodial branches (USB, >10th branch). Mean was used for study), mainstem internodes length (MIL, cm) (The MIL was divided into four groups (Fig. 1A): The 1st group included the nodes from the bottom up to the squaring stage (usually 1st–7th node); the remaining part was evenly divided into the 2nd (8th–12th node), 3rd (13th–17th node), and 4th (>17th node) groups. Mean was used for study), number of bolls per plant, Boll weight (g) (five random bolls from a single plant were weighed), and seed cotton yield per plant (g) were considered for the study. The method of evaluation of eleven traits such as compact plant architecture and yield traits suitable for mechanical harvesting and high-density planting can be found in Fig. 1

Statistical analysis

The statistical analysis of data was carried out using R-Studio (v.4.2.3). According to Panse and Sukhatme (1962), the pooled analysis of variance (ANOVA) was calculated using mean values. The Tukey's honesty significance difference (HSD) test was implemented through the 'Agricolae' R package (de Mendiburu and de Mendiburu 2019) to compare significant differences at $p \leq 0.05$ among the pooled mean. The Bartlett test (Anderson and McLean 2018) was carried to testing the homogeneity of error variances across locations using the 'bartlett test' R package. The pooled combining ability ANOVA and their effects were conducted following Griffing's (1956) method 2 model 1 (fixed effects), using AGD-R, CIMMYT software (v.3.0). The significance of GCA and SCA sources of variation was determined using the error term. Prior to estimating the genetic variations, assumptions of diallel analysis were verified using the 't^2' test for the uniformity of Wr (Covariance between parents and offspring) and Vr (Variance of array). The presence or absence of epistasis was assessed through the 'b' (regression) of Wr on Vr. The genetic components were estimated following the

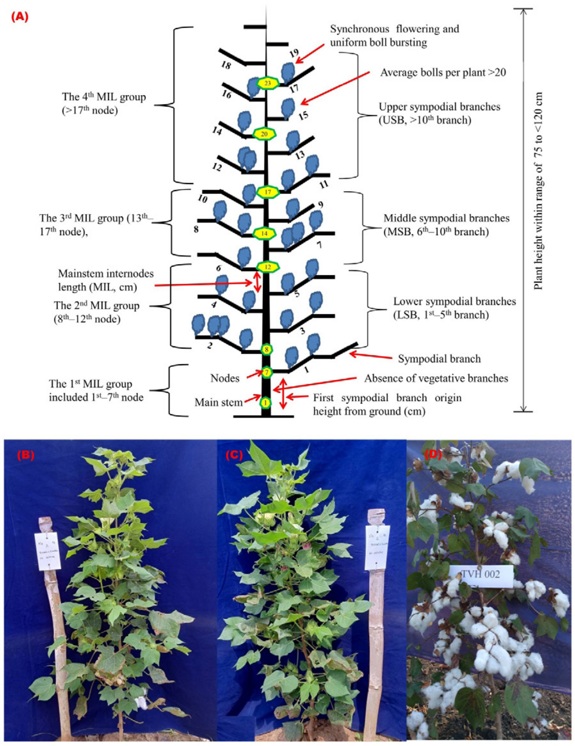

Fig. 1. A = Ideal cotton plant architecture traits amenable for mechanical harvesting (Spindle and Stripper pickers) and high density planting. B and C = Field view of cross TVH002 × Suraksha in E_1 and E_2, C= TVH002 plant

Hayman's (1954) graphical approach. Correlation matrices for studied traits in pooled environments were generated using the 'Corrplot' R-package (Wei et al. 2017).

Results and discussion

ANOVA of combining ability effects in pooled environment

The ANOVA of mean squares which is aimed to assess combining ability effects on various traits were presented in Table 2. Significant genetic variation was found for all traits, indicating potential for improved selection outcomes (Bourgou et al. 2022; Chaudhari et al. 2023). The *gca* and *sca* effects interacted significantly with the environment, except for trait bolls per plant and height of first sympodial branch origin. Notably, GCA and SCA ratios varied across traits, between 0.19 for number of monopodia branches and 518.79 for seed cotton yield. Except for monopodial branches, mainstem internodal length, and boll weight, all traits exhibited GCA/SCA ratios greater than unity which indicated a high potential for breeding progress and it was consistent with the findings of Simon et al. (2013). It was observed that error variances across locations are homogenous for studied traits. The Bartlett's 'k' squared values and pooled RCBD-ANOVA is given in Table 3. The genotypes were differed significantly, reflecting substantial trait variability and environment variability accounted for the largest portion of this variability for most traits followed by genotype variability.

Mean performance of genotypes over two environments

The mean performance for genotypes (parents and offspring) is presented in Table 4. The days to 50% flowering ranged from 46.00 to 56.67 days as observed in CO17 × Nano and NDLH193, respectively with overall mean days of 51.12. The trait plant density varied from lowest number of pants from 6.95 (plants/sq.m) to highest plants of 12.49 as recorded by Suraksha and TVH002× CO17, respectively with an average value of 9.86. The least value of plant height was recorded at 80.00 cm (TVH002 × Nano) whereas the highest value of plant height's 101.00 cm was observed in NDLH1938 and with an average height of 90.19 cm. Monopodial branches ranged from 0.47 to 1.20 (nos.) with an average value of 0.83 (nos.). The maximum number of monopodia per plant was observed in parent NDLH1938, whereas the minimum was found from the parent TVH002. Mean values for height of first sympodial branch origin among the genotypes varied from 17.98 (NDLH1938) to 25.82 cm (TVH002 × Nano) with an average height of 22.36 cm. The mechanical harvesters most preferred the exceed length > 20 cm within a plant height range of 75 to <120 cm. The present findings support the previous results of Van der Sluijs (2015) and Yan et al. (2019).

Table 1. A list of genotypes used in the study with their pedigree and the main characteristic features

Variety	Pedigree	Origin/Source	Characteristic features of parents
TVH002	Suraj × TCH1819	CRS-Veppanthattai	High yielding compact, short duration, medium staple fibre (MSF), and moderately leafhopper resistant (MLR)
CO17	Khandwa 2× LH220	DC-Coimbatore	Compact, early maturity, MSF, and susceptible to leafhopper
NDLH1938	NDLH 1797 X NDLH 1325	RARS-Nandyal	High yielding, resistant to leafhopper (LR), and MSF
Suraksha	Surabhi × (MCU5 × Z2)	CICR-Coimbatore	High yielding semi compact variety, superior fibre quality, medium size bolls, LR, and high ginning outturn
Nano	CCH 526612 X VNWH-1	CICR-Coimbatore	MLR, MSF, high yield, and short plant stature

CRS = Cotton Research Station; DC = Department of Cotton; RARS = Regional Agricultural Research Station; CICR = Central Institute for Cotton Research.

Table 2. Pooled ANOVA mean squares for combining ability of eleven traits

Traits	GCA	GCA × ENV	SCA	SCA × ENV	GCA/SCA	Error
	(df = 4)	(df = 4)	(df = 10)	(df = 10)	(df = 14)	(df = 56)
DFF (days)	67.24**	5.75**	20.64**	6.08**	33.95**	2.66
PD (sq.m)	55.51**	0.87**	6.86**	0.44	20.76**	0.69
PH (cm)	335.52**	121.69**	64.42**	12.90**	141.87**	5.45
NMB (nos.)	0.45**	0.17**	0.08**	0.15**	0.19**	0.01
FSB (cm)	22.68**	2.15ns	29.69**	1.37ns	27.69**	1.49
NSB (nos.)	9.61**	1.43**	3.35**	1.28**	5.14**	1.43
SBL (cm)	59.97**	4.12**	15.38**	4.36**	28.12**	3.55
MIL (cm)	0.25**	0.03ns	0.28**	0.07**	0.27**	0.02
BP (nos.)	22.94**	0.09ns	9.24**	0.05ns	13.16**	2.16
BW (g)	1.07**	0.44**	0.57**	0.30**	0.71**	0.07
SCY (g)	599.22**	61.58**	486.61**	209.89**	518.79**	5.74

** Significant at $p \leq 0.01$; ns = Non-significant; df = Degrees of freedom; GCA =General combining ability; SCA = Specific combining ability. GCA × ENV = Interaction of GCA and environment; SCA × ENV = Interaction of SCA and environment; DFF = Days to 50% flowering; PD = Plant density; PH = Plant height; NMB = Number of monopodia branches; FSB = height of first sympodia branch origin; NSB = Number of sympodia branches; SBL = Sympodial branch length; MIL = Mainstem internodal length; BP = Boll per plant; BW = Boll weight; SCY = Seed cotton yield per plant.

Table 3. The pooled RCBD-ANOVA for eleven traits

Traits	Environment (E)	Genotype (G)	Replication within E	G × E	Error	Bartlett's K- Squared
	(df = 1)	(df =14)	(df = 4)	(df = 14)	(df = 56)	
DFF	53.26**	36.37**	1.07*	8.62**	2.66	0.15
PD	0.51**	25.12**	15.69***	0.52**	0.65	1.99
PH	136.48**	209.3**	6.57**	17.16**	5.45	1.12
NMB	0.32***	0.20***	0.07ns	1.62***	0.01	1.75
FSB	5.89ns	39.56**	0.59ns	1.67**	1.35	0.34
NSB	45.7**	15.96**	3.90**	.4.46ns	1.43	0.03
SBL	160.46ns	32.57**	2.72*	6.90**	3.55	2.86
MIL	0.01ns	0.25**	0.05**	0.05**	0.01	0.67
BP	6.76**	16.58ns	2.92**	8.44**	2.16	0.04
BW	2.23**	0.66*	0.02ns	0.35**	0.07	0.17
SCY	50917.78**	121.41**	2.80*	42.69**	1.21	1.54

*, and **, Significant at $p \leq 0.05$ and $p \leq 0.01$, respectively; ns = Non-significant.

Number of sympodial branches per plant varied from 19.36 (NDLH1938) to 24.50 (TVH002 × CO17), with an average value of 22.56. The range of variation for sympodial branch length was recorded from 17.51 cm (TVH002 × CO17) to 27.84 cm (NDLH1938) with an overall mean length of 21.23 cm. The lowest mainstem internodal length per plant was recorded for cross TVH002 × Suraksha (5.22 cm), and the highest length was 6.04 cm (Suraksha). The mean length of this trait was 5.59 cm.Bolls per plant ranged from 21.35 to 28.58 (nos.), with an overall mean of 25.04 (nos.). The highest bolls were observed in genotype Suraksha, and the lowest value was found from NDLH1938.The cross-performance value for average boll weight ranged from 3.56 g (NDLH1938 × Nano) to 5.10 g (TVH002 × CO17) with an overall weight of 4.37 g. The performance of genotypes for seed cotton yield per plant ranged from 92.74 g (NDLH1938) to 126.60 g (TVH002 × Nano) with an overall mean yield of 110.27 g. Overall hybrids exhibited lower mean values for plant architecture traits such as flowering days, plant height, monopodial branch, sympodial branch and internodal length when compared

Table 4. Pooled mean performance of cotton genotypes for eleven traits

Genotypes	DFF	PD	PH	NMB	FSB	NSB	SBL	MIL	BP	BW	SCY
TVH002	46.91hi	10.82bc	84.00i-k	0.47j	22.56de	23.02a-e	20.63d-h	5.60c-e	24.74b-d	4.22d-f	105.61b-e
CO17	52.70c-f	11.16b	87.33hi	0.83e-g	23.13c-e	22.42a-e	20.46d-h	5.67c-e	25.04b-d	4.23c-f	101.90de
NDLH1938	56.67a	7.26f-h	101.00a	1.20ab	17.98ij	19.36g	27.84a	5.96ab	21.35fg	4.22d-f	92.74e
Suraksha	54.18a-e	6.95gh	98.03a-d	1.17a-c	19.36g-i	21.64c-f	26.23ab	6.04a	28.58a	4.51b-e	109.56b-d
Nano	51.33e-g	8.60de	92.17e-g	1.00c-e	19.84gh	22.01b-e	23.48b-d	5.71b-e	22.68d-f	3.71gh	101.62de
Parental mean	52.36	8.96	92.51	0.93	20.57	21.69	23.73	5.80	24.48	4.18	102.29
TVH002 × CO17	46.44i	12.49a	81.67jk	0.50ij	24.45a-c	24.50a	17.51h	5.51d-f	28.64a	5.10a	106.57b-d
TVH002 × NDLH1938	47.67hi	10.82bc	81.00jk	0.90d-f	22.97c-e	22.60a-e	18.93e-h	5.32fg	24.91b-d	3.69gh	114.86a-d
TVH002 × Suraksha	53.00b-e	9.33d	93.50d-g	0.78f-h	21.81ef	23.69a-d	21.75c-g	5.22g	24.40b-e	5.02a	118.67a-c
TVH002 × Nano	49.67f-h	11.34b	80.00k	0.67g-i	25.82a	23.81a-c	18.33f-h	5.53c-f	25.66bc	4.66a-d	126.60a
CO17 × NDLH1938	52.00d-f	10.49bc	92.33e-g	0.71gh	22.71de	23.30a-e	21.08d-h	5.54c-f	25.51bc	3.87f-h	101.05de
CO17 × Suraksha	54.20a-e	10.23c	91.00f-h	0.67g-i	23.81b-d	22.56a-e	18.40f-h	5.55c-f	26.14a-c	4.71a-c	112.09a-d
CO17 × Nano	46.00i	12.47a	89.67gh	0.60h-j	20.67fg	23.92ab	18.04gh	5.46e-g	27.01ab	4.62a-d	120.03a-c
NDLH1938 × Suraksha	54.00a-e	7.18d	100.00ab	1.17a-c	23.22c-e	22.94a-e	24.28a-d	5.70b-e	21.98e-g	4.69a-d	118.45ab
NDLH1938 × Nano	53.67a-e	10.78bc	96.00b-e	1.10bc	22.09ef	21.12e-g	21.50c-h	5.63c-e	23.98c-e	3.56h	104.87c-e
Suraksha × Nano	48.40g-i	8.02ef	85.10ij	0.63h-j	24.92ab	21.52d-f	22.46b-f	5.48e-g	24.97b-d	4.72ab	119.45a-c
Hybrid mean	50.50	10.32	89.03	0.77	23.25	23.00	20.23	5.49	25.32	4.47	114.26
Grand Mean	51.12	9.86	90.19	0.83	22.36	22.56	21.39	5.59	25.04	4.37	110.27
SE ± m	0.98	0.88	1.43	0.06	0.69	0.70	1.25	0.13	0.81	0.15	2.65
CV (%)	3.27	7.73	2.72	11.09	5.97	5.17	9.85	4.00	5.69	6.00	10.93

SE ± m = Standard error mean; CV = Coefficient of variation. No significant differences among means with the same letter in each column

to the parents. This suggests that hybrids displayed early maturity and compact plant canopy which accommodated more plants per unit area (Gunasekaran et al. 2020) and absorbed superior performance in terms of yield. The higher plant densities directly cause positive yield has also been reported (Yan et al. 2019; Raza et al. 2013; Abro et al. 2009).

GCA and SCA effects

Despite the limited number of parents included in the crossing, gca effects revealed significant variation in a pooled environment (Table 3). Parents *viz*., TVH002, CO17 and Nano had *gca* effect in negative direction for flowering and architecture traits such as plant height, monopodia, sympodial branch and internodal length indicating that they are good general combiners for earliness and compact canopy. However, TVH002 and CO17 were acts as good combiners with higher positive effects for plant density, first sympodial origin and sympodial branches and can be used in hybridization to develop suitable architecture traits for mechanical harvesting. Suraksha identified the best combiner for bolls/plant, boll weight and yield. Genotypes demonstrated promising potential for study traits that vary, justifying their inclusion in the diallel to generate hybrids with a broad genetic base (Bourgou et al. 2022). It observed that earliness and architecture traits can reduce water requirements (Cheatham et al. 2003) and enhance mechanization (Yan et al. 2019). The results suggest that, except Suraksha and NDLH1938 remaining genotypes exhibited controlled vegetative growth. Similar findings were reported by Simon et al. (2013), indicating that additive effects predominantly influence these traits. However, Vasconcelos et al. (2018) concluded that dominance effects play a significant role in these traits under water stress conditions.

The *sca* effects of evaluated hybrids are presented in Table 5. The sca effect for day to flowering revealed that cross between CO17 × Nano recorded highest sca effects in desirable negative direction followed by TVH002 × NDLH1938

Table 5. Estimation of combining ability effects on genotypes for eleven traits in pooled environment

Genotypes	DFF	PD	PH	NMB	FSB	NSB	SBL	MIL	BP	BW	SCY
GCA on Parents											
TVH002	-2.30**	0.92**	-5.28**	-0.17**	0.86**	0.76**	-1.51**	-0.11**	0.41ns	0.10ns	2.33**
CO17	-0.38ns	1.26**	-0.30ns	-0.12**	0.54**	0.54*	-1.77**	-0.02ns	1.02*	0.08ns	-2.58**
NDLH1938	1.99**	-0.77**	4.32**	0.19**	-1.03**	-0.96**	1.87**	0.08**	-1.60**	-0.28**	-5.27**
Suraksha	1.60**	-1.50**	3.51**	0.09**	-0.24*	-0.20ns	1.57**	0.07**	0.63*	0.28*	3.74**
Nano	-0.90*	0.09ns	-2.24**	-0.15**	-0.14ns	-0.14ns	-0.15*	-0.01ns	-0.47ns	-0.18*	1.79**
SCA on Hybrids											
TVH002 × CO17	-1.99*	0.45*	-2.94*	-0.04ns	0.69ns	0.65ns	-0.60ns	0.05ns	2.17**	0.55**	-3.45**
TVH002 × NDLH1938	-3.54**	0.79*	-8.22**	-0.19**	0.78ns	0.24ns	-2.82*	-0.24**	1.06*	-0.50**	7.53**
TVH002 × Suraksha	2.58*	0.05ns	5.09ns	0.03ns	-1.17*	0.57ns	0.30ns	-0.33**	-1.68*	0.27ns	2.34**
TVH002 × Nano	1.75*	0.47*	-2.67**	0.00**	2.74**	0.64*	-1.40ns	0.05ns	0.68*	0.37ns	12.21**
CO17 × NDLH1938	-0.73ns	0.13ns	-1.87ns	-0.19**	0.84*	1.16**	-0.41*	-0.11**	1.04*	-0.30*	-1.36**
CO17 × Suraksha	1.86*	0.61*	-2.39*	-0.13**	1.15*	-0.34*	-2.79**	-0.09*	-0.55*	-0.02*	0.67**
CO17 × Nano	-3.83**	1.26**	2.02**	-0.12**	-2.09**	0.96**	-1.42**	-0.11**	1.41ns	0.35ns	10.55**
NDLH1938 × Suraksha	-0.72ns	-0.41*	1.99ns	0.06**	2.13**	1.53*	-0.56*	-0.04ns	-2.10**	0.32*	9.72**
NDLH1938 × Nano	1.46ns	1.60**	3.74**	0.08*	0.90*	-0.35ns	-1.61**	-0.03ns	1.00ns	-0.35*	-1.92**
Suraksha × Nano	-3.42**	-0.43*	-6.35**	-0.29**	2.94**	-0.70*	-0.35**	-0.18**	-0.23*	0.25ns	3.65**

*, ** and ns indicates significant at $p \leq 0.05$, $p \leq 0.01$, and non-significant, respectively

indicating that these are the best crosses for earliness only. The hybrid TVH002 × NDLH1938 is best combiner for plant height and sympodial length with negative *sca* effects. The hybrid TVH002 × Nanois best combiner for first sympodial origin, boll weight and seed cotton yield with high positive effects. Eight hybrids displayed a negative *sca* effect for sympodia and internode length, suggesting a compact form suitable for mechanization (Yan et al. 2019). The *sca* effects for remaining architecture and yield traits can found in Table 4. From the previous section, it is understood that the involvement of parents *viz.*, TVH002, CO17 and Nano in crosses is said to be best combiners for compact traits. This may be due to more parental contributions of favorable alleles from any or both parents in progenies. Similar effects were also reported by Cheatham et al. (2003) and Simon et al. (2013). Previous studies have indicated that a narrow genetic base with common parental ancestry can lead to unfavorable sca effects (Khan 2013; Raza et al. 2013). Results of sca effects indicate that the hybrids were outperformed than parents for most traits. Selection for these traits should be based on evaluations across multiple environments (Raza et al. 2013). In an experiment Murthy and Pradeep (2022) identified stable cotton genotypes amenable to a high-density planting system. They found that the heterozygotes were found more stable due to individual buffering capacities over homozygotes. A few hybrids showed a strong association between heterobeltiosis and specific combining ability. The findings of Patil et al. (2017) also supported the results on the performance of heterozygotes which they observed as greater than that of homozygotes due to individual buffering capacities that leads to increased yields and stability of hybrids than parents.

Graphical approach

The ‘t^{2}’ values were estimated for traits in pooled environments and all traits were not showed significance (Table 6). The traits exhibited significant ‘t^{2}’ values indicating a deviation from assumptions in diallel analysis (Hussain et al. 2019; Mather 1982). Therefore, Wr-Vr uniformity values are estimated. The analysis of gene effects demonstrated that both additive (D) and dominance (H_1 and H_2) components played a significant role in governing the traits. The dominance gene effect having a greater impact on trait control (Karademir and Gencer in 2010). However, for certain traits, only the dominance components were found to be significant, while the additive component did not show significance for NMB (0.07%), MIL (0.02%), and BW (0.07%). This indicates that dominance genes solely governed these specific traits are in agreement with the earlier findings of Basal and Turgut (2003).

Average degree of dominance $(H_1/D)^{0.5}$) ratio were >1 for traits, indicating the presence of over dominance ranging from 1.13% (DFF) to 2.70% (SCY), except for PD, NMB and NSB which exhibited a dominance effect. Vasconcelos et al. (2018) and Hussain et al. (2019) were reported dominance ratio <1 for traits was influenced by dominance genes.

Table 6. Estimates of the genetic components uniformity of Wr-Vr and heritability values for eleven traits in pooled environment

Parameters	DFF	PD	PH	NMB	FSB	NSB	SBL	MIL	BP	BW	SCY
t^2 value	2.56	2.10	1.19	0.73	1.88	2.47	2.48	1.05	2.45	0.45	2.23
b (Regression)	0.76$$	0.61$+	0.71$$+	0.48$++	0.01++	0.28$+	0.93$$	0.77$$	-0.05++	0.38+	0.72$$+
E	2.70	0.69**	4.78**	0.02*	1.49**	1.47**	1.30**	0.02	1.93	0.07	5.74**
D	9.00**	3.14**	28.40**	0.07	3.32**	0.22**	8.69**	0.02	0.81**	0.08	33.16**
F	2.10**	-2.37*	-20.88**	0.00	3.08**	-2.06*	0.92	0.01	2.14**	-0.06	-16.98**
H_1	11.47**	2.09**	46.38**	0.16*	12.82**	0.53*	9.21**	0.10*	4.18**	0.52*	242.13**
H_2	9.98**	1.82**	47.13**	0.14*	12.08**	0.42**	8.64**	0.10*	2.17**	0.40*	224.11**
h^2	3.45	4.27**	36.37**	0.04	17.32**	4.78**	27.40**	0.23	-1.21	0.10	363.77**
$(H_1/D)^{0.5}$	1.13	0.82	1.28	0.97	1.96	1.25	0.97	2.26	2.27	2.62	2.70
KD/KR	1.23	0.37	0.55	1.06	1.62	-0.95	1.12	1.16	3.77	0.72	0.83
h^2/H_2	0.35	2.35	0.77	0.91	1.43	11.35	3.17	2.30	-0.56	0.25	1.62
$H_2/4H_1$	0.22	0.22	0.25	0.17	0.24	0.20	0.23	0.24	0.13	0.19	0.23
σ^2A	4.20	2.89	24.26	0.04	0.49	0.79	3.67	0.01	0.34	0.13	34.09
σ^2G	6.69	3.35	36.05	0.05	3.51	0.90	5.83	0.03	0.88	0.23	90.11
σ^2P	9.39	4.04	40.83	0.07	4.99	2.37	7.13	0.05	2.81	0.29	95.85
h^2n (σ^2A/σ^2P)	0.45	0.72	0.59	0.55	0.10	0.34	0.51	0.16	0.12	0.44	0.36
h^2b (σ^2G/σ^2P)	0.71	0.83	0.88	0.70	0.70	0.38	0.82	0.67	0.31	0.78	0.94

E = Environmental variance; D = Additive effect; F = Mean Fr over array; H_1 = Dominance effect; $H_2 = H_1[1-(u-v)^2]$; h^2 = Heritability; $(H1/D)^{0.5}$ = Mean degree of dominance; KD/KR = $\{(4DH_1)^{0.5} + F\hat{}\}/\{(4DH_1)^{0.5} - F\hat{}\}$ ratio of dominant & recessive genes in parents; h^2/H_2 = Number of gene groups; $H_2/4H_1$ = Proportion of genes with +/- effects in parents; σ^2A= Additive variance; σ^2G = Genotypic variance; σ^2P = Phenotypic variance; h^2n = Narrow-sense heritability; h^2b = Broad-sense heritability. (*, **) Significance at 5% and 1% levels, respectively; ($, $$) Significance at 5% and 1% levels, respectively, for Ho: b = 0; (+, ++) Significance at 5% and 1% levels, respectively, for Ho: b = 1.

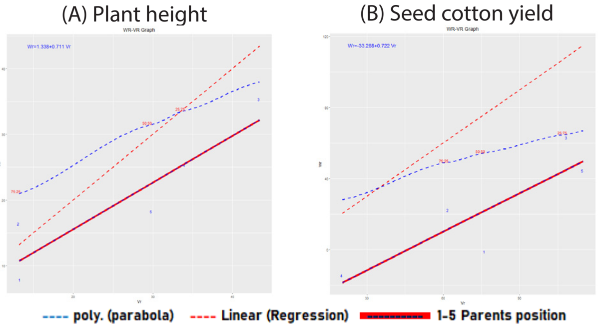

Fig. 2. Wr-Vr graph. Blue colored numerical 1-5 indicates parental genotypes (1 = TVH002; 2 = CO17; 3 = NDLH1938; 4 = Suraksha; 5 = Nano)

Overall, non-additive gene actions were the predominant factors governing the expression of architecture and yield and its attributing traits under favorable environments also reported by Karademir and Gencer, 2010 and Chaudhari et al. 2023.

Asymmetrical distribution of alleles was observed with an $H_2/4H_1$ ratio <0.25, indicating an excess of dominant genes in traits. Some traits, such as PD, PH, NSB, BW, and SCY, were controlled by multiple recessive genes, as evidenced by negative values of F and KD/KR <1. In contrast, other

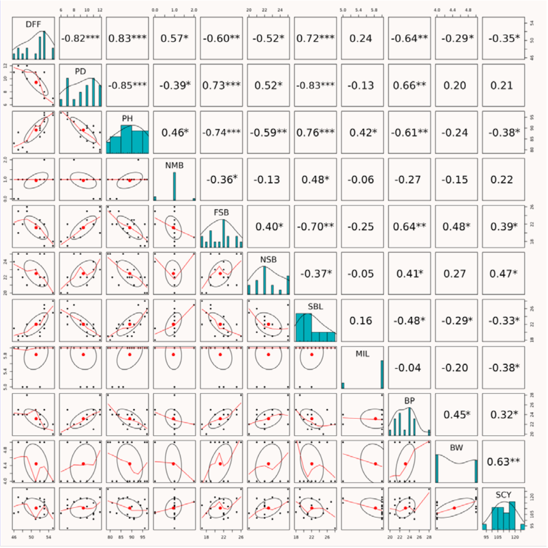

Fig. 3. Correlation pairs plots (upper panels with numerical indicates positive or negative correlations), frequency distribution (diagonal panels) and scatter plots (lower panels). *, **, *, indicates significant at p ≤ 0.05, p ≤ 0.01, p ≤ 0.001, respectively. DFF = Days to 50% flowering; PD = Plant density; PH = Plant height; NMB = Number of monopodia branches; FSB = height of first sympodia branch origin; NSB = Number of sympodia branches; SBL = Sympodial branch length; MIL = Mainstem internodal length; BP = Boll per plant; BW = Boll weight; SCY = Seed cotton yield per plant**

traits exhibited positive values of F and KD/KR >1, indicating control by multiple dominant genes and this deviations of gene actions was also confirmed in earlier findings of by Vasconcelos et al. (2018) and Chaudhari et al. (2023). The h^2/H_2 values <1, suggesting the presence of at least one dominant gene governing traits (DFF, PH, NMB, BP and BW) and other traits were may controlled by recessive genes. Positive and significant h^2 estimates indicated a dominant gene effect across loci in most studied traits. Patel and Kathiria (2018) reported the specific dominant gene group could not be determined due to positive or non-significant h^2 values. In our study we found such estimates for traits *viz*., DFF, NMB, BP, and BW.

Additionally, epistatic gene effects were investigated, the alignment of array points on the Wr-Vr graph with the unity line indicated that the regression 'b' value deviated significantly from zero, not from one. These findings strongly suggested the absence of epistatic effects (Mather 1982). In pooled graphical analyses, the regression line exhibited various patterns for each trait. We displayed graphs of plant height and seed cotton yield only (Fig. 2). In Figs. 2A and 2B, the regression line was intersected by the Wr axis above the origin and touching the parabola, indicating partial dominance. Among the parents, TVH002 and C017 for plant height and Suraksha for seed cotton yield had a higher frequency of dominant genes, as these parents occupied the nearest position to the origin of the regression line. Accordingly, the parent NDLH1938 for PH and SCY, and Nano for SCY had a higher frequency of recessive genes. These occupied the farthest position from the origin, whereas Suraksha, and Nano for PH, and CO17 and NDLH1938 for SCY had an equal proportion of dominant and recessive genes as they occupied an intermediate position. These findings align with Patel and Kathiria (2018) and Hussain et al. (2019).

Estimates of heritability

Heritability was calculated using additive, genotypic and phenotypic variances (Table 5). Among the traits, seed cotton yield had a very high variances ($\sigma^2A = 34.09$; $\sigma^2P = 95.85$; $\sigma^2G = 90.11$), followed by plant height. We observed that phenotypic variance is generally higher than other measured variances for the same traits. Bhateria et al. (2006) classified the heritability estimates into high (>0.50), medium (0.30–0.50), and low (<0.30). In our study, maturity trait days to flowering expressed medium h^2n (0.45) and high h^2b(0.71). For architectural or compact traits both types of heritability exceed the medium ranges, it was exceptional to traits NSB, FSB, and MIL. It indicates that selection is more effective for earliness and architectural traits with high heritability and was predominantly controlled by the dominance gene effect. These traits should be easily inherited in progenies, similar results foundby Patel and Kathiria (2018). Similarly selection was more effective for seed cotton yield and boll weight. Trait with low ranges should require evaluation in multiple environments. These results are consistent with the findings of Cheatham et al. (2003) and Huangjun and Meyers (2011), confirming the potential for trait improvement through breeding efforts.

Correlation analysis

Correlations among traits in pooled environments are depicted in Fig. 3. Days to 50% flowering was negatively significant correlation with bolls/plant and seed cotton yield (r = -0.35*). Plant height was significantly negative correlation with seed cotton yield (r = -0.38*), bolls/plant, sympodial branches (r = -0.59**) and height of first sympodial origin (r = -0.74**), and positive association with length of sympodial branch (r = 0.76**) and mainstem internode length (r = 0.42*). It implies that earl maturing, shorter and compact plants with a narrower height range (75 to <120 cm) may offer increased boll retention, escape from drought stress, and produce more stable yield across environments (Yan et al. 2019). However, plant density was significantly negative correlation with monopodial branch (r = -0.39*) and sympodial branch length (r = -0.83**).

An increasing monopodial branches reduced yield and slightly affected the yield components (Van der Sluijs 2015). Our results suggest that longer internodes and sympodial lengths contribute to robust and taller plants. However, such plant architecture can pose challenges in agronomic practices. The shorter internode length was often accompanied by larger roots during early growth, leading to improved water and nutrient uptake to upper bolls were not yet fully developed (Fernandez et al. 1991; Kerby et al. 2010). And also lesser monopodia and shorter sympodial lengths accommodate more plants per unit area (1.2 lakhs/ha), which is best suitable for high density planting with a recommended spacing of 90/60 × 30/15 cm (Gunasekaran et al. 2020; Venugopalan et al. 2011). Our findings provide valuable insights for crop management and breeding strategies, particularly in the context of high-density cotton planting and mechanical harvesting.

Author's contribution

Conceptualization and coordination of research work (SS, BM, and SM); resources (SS, SM, and SR); methodology (SS, BM, and SM); data collection, formal analysis and writing-original draft preparation (BM); writing-review and editing (BM, SS and SM); supervision (SS). All authors have read and agreed to the published version of the manuscript.

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